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The role of tolerance variation in vulnerability forecasting of insects

Sarah E Diamond and Aaron R Yilmaz

Quantifying the amount of climatic change organisms can withstand before exceeding their physiological tolerance is a cornerstone of vulnerability forecasting. Yet most work in this area treats tolerance as a fixed trait. We review recent work that quantifies variation in high temperature tolerance across bioclimatic gradients, and we explore the implications for vulnerability to climate change. For some sources of variation, including differences in the evolutionary potential of heat tolerance across latitude, the typical biogeographic pattern of high vulnerability in the tropics is exacerbated. For other sources of variation, including certain types of plastic variation in heat tolerance, the biogeographic pattern of high tropical vulnerability is diminished. As a consequence, thermal tolerance variation should not be ignored in vulnerability forecasting.

Address
Department of Biology, Case Western Reserve University, Cleveland, OH 44106, USA

Corresponding author: Diamond, Sarah E (sarah.diamond@case.edu)

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Forecasting vulnerabilities to climate change with tolerance traits

Insects provide critical ecosystem services that support biodiversity and human well-being [1]. However, several recent studies point to an alarming rate of decline in insect populations over the last several decades [2]. In some cases, these declines have occurred even within protected areas and are not a direct consequence of habitat loss [3], but rather point to the effects of recent climate change. As humans continue to modify the environment, insect declines are likely to increase in the future [4]. The ability to forecast insect declines, with respect to species identity and geographic location, is therefore of paramount importance, as this information that can be used by conservation planners to help mitigate insect declines [5,6]. How best to forecast insect responses to global change remains an area of active research and debate [7].

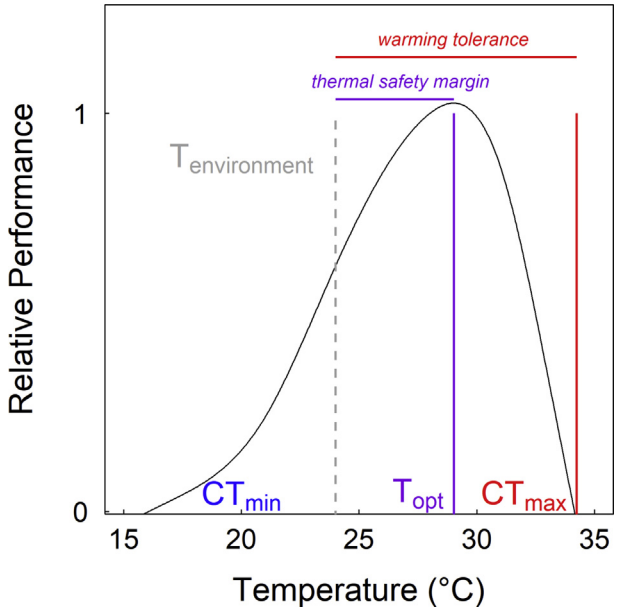
Trait-based approaches have met with considerable success, especially those which examine the relationship between temperature change — a hallmark of global change — and thermal physiological traits [[9•]]. However, a major shortcoming of these approaches is that they treat the tolerance traits as fixed, when in reality, trait values can shift as individuals remodel their physiology under different environmental conditions within a generation (phenotypic plasticity) or as populations exhibit changes in their mean tolerance across generations (evolutionary change) [9•]. Here we review current biogeographic patterns of thermal tolerance in insects, and explore the implications of these patterns with respect to insect vulnerability to global climate change. We further consider how plastic and evolved variation in thermal tolerance might influence forecasts of vulnerability to global change.

Thermal physiology-based measures of vulnerability: metrics and patterns

Ectothermic species tend to exhibit stereotypical performance responses to temperature, where performance rises from some lower threshold temperature up to a thermal optimum, at which performance is greatest, before declining sharply until the upper threshold is reached [10]. The difference between measures of heat tolerance (such as the lethal thermal limit or the critical thermal maximum, CT_{max}, which defines the loss of coordinated movement) and environmental temperature are broadly termed 'warming tolerance' and have been used extensively to assess the vulnerability of insects (and closely related arthropods) to global climate change. Relatedly, the difference between environmental temperature and the thermal optimum is called the 'thermal safety margin' and has been used in a similar manner to estimate how much of a thermal buffer an organism has before becoming vulnerable to climate change [11,12,13,14,15••,16] (Figure 1, Box 1, Table 1).

The emerging biogeographic picture from the current research is one of increased vulnerability of tropical insects [16]. This pattern appears to be driven by species at low latitudes exhibiting narrow thermal tolerance breadths (the range between cold and heat tolerance), which places them very close to their thermal optimum and heat tolerance relative to the environmental

Figure 1



Thermal performance curve, indicating cold tolerance (as assessed by the minimum critical temperature for performance, CT_{min}); heat tolerance (as assessed by the maximum critical temperature for performance, CT_{max}); thermal optimum (T_{opt}, the temperature at which performance is greatest). Environmental temperature is shown in the dashed line, and vulnerability indices are presented relative to $T_{environment}$: thermal safety margin is the difference between T_{opt} and $T_{environment}$, and warming tolerance is the difference between CT_{max} and $T_{environment}$.

Box 1 Glossary of terms.

Descriptors of thermal performance and vulnerability

Thermal tolerance – the upper or lower endpoint of performance across a range of environmental temperatures, and a key trait in vulnerability forecasting with organismal physiology

CT_{max} — the critical thermal maximum, often defined by the (upper) temperature at which coordinated activity is lost; a commonly used measure of heat tolerance, and which forms the basis for many assessments of warming tolerance

CT_{min} — the critical thermal minimum, often defined by the (lower) temperature at which coordinated activity is lost

T_{opt} — the optimal temperature at which performance is maximized for a given response, and which forms the basis for assessment of the thermal safety margin

Thermal safety margin — the difference between the thermal optimum and environmental temperature

Warming tolerance — the difference between a measure of heat tolerance and environmental temperature

Microclimate — the climatic conditions nearer to those that organisms inhabit rather than air temperature at a height of 2 m in the shade as is the basis for most warming tolerance assessments, for example, from climatic databases such as WorldClim

Mechanisms underlying variation in thermal tolerance

Plasticity — remodeling of an organism's thermal tolerance within a generation; for example, exposure to a warmer temperature environment which increases the expressed heat tolerance trait value

Evolutionary change — shifts in tolerance trait values across generations; here, we are specifically interested in allele frequency changes over generations, as contrasted with, for example, maternal effects which also manifest across generations

Evolutionary potential — a general term that describes the potential for a trait to evolve based on the amount of additive genetic variation; for example, narrow-sense heritability (the amount of additive genetic variation divided by the total phenotypic variation) is a common measure of evolutionary potential

Genetic accommodation — a process by which unexpressed genetic variation is revealed under novel environments and selection then acting on this variation; an example of the potential interaction between plastic and evolutionary mechanisms that generate variation in tolerance traits under climate change

temperatures that they currently experience and will experience in the future [13]. Despite the smaller anticipated magnitude of climate warming at lower compared with higher latitudes, the negative consequences of narrow thermal tolerance breadths at lower latitudes is sufficient to overwhelm the effects of diminished warming [11]. Higher latitude species are generally less vulnerable to climate change because they have broader ranges of thermal tolerance and are much farther from their thermal optimum and upper thermal tolerance. Yet while these forecasts of vulnerability allow environmental temperature to shift (e.g. by comparing warming tolerance under current and future climates), the tolerance traits are treated as fixed. Below we consider the sources of variation in insect thermal tolerance and how this variation might alter vulnerability assessments. Specifically, we consider intraspecific sources of variation in tolerance including plastic and evolved differences in tolerance across space and time, and then summarize the patterns across different insect species and biogeographic regions, as these are the levels at which warming tolerance analyses are typically performed. Of particular interest is whether the consideration of tolerance variation quantitatively, or perhaps even qualitatively, alters assessments of vulnerability to climate change as compared with assessments derived from mean trait values. In the case of such alterations, global to local-scale patterns of vulnerability based on trait means could be inaccurate, with downstream consequences for conservation planning and management.

Ecological and evolutionary sources of variation in tolerance traits

The critical importance of variation in tolerance has come into sharper focus over the past several years. A striking example comes from Bush and colleagues [17] — using a species distribution modeling approach which incorporated empirical estimates of variability heat tolerance, they found qualitatively different forecasts of vulnerability to climate change compared with models that excluded this variation. Specifically, for several of the

Table 1

List of studies on insect (and closely related arthropod) warming tolerances and thermal safety margins

Study	Vulnerability metric(s)	Description
Allen *et al.* 2016 [15••]	Warming tolerance	6 species of springtails across a wide spatial extent from the tropics to the arctic; considers the interactive effects of rearing temperature and rate of temperature change on thermal tolerance and how this variation influences warming tolerance
Bonebrake *et al.* 2012 [12]	Warming tolerance, thermal safety margin	38 species of insects at a global scale; considers spatial heterogeneity in the habitat
Deutsch *et al.* 2008 [11]	Warming tolerance, thermal safety margin	38 species of insects at a global scale
Diamond *et al.* 2012 [14]	Warming tolerance	156 species of ants at a global scale
Hoffmann *et al.* 2013 [16]	Warming tolerance, thermal safety margin	173 species of insects at a global scale
Sunday *et al.* 2014 [13]	Thermal safety margin	70 species of insects at a global scale; considers operative body temperature rather than air temperature

drosophilid species they studied, the incorporation of tolerance variation (allowing tolerance to evolve in response to climatic warming) reduced the projected future vulnerability. Yet the role of variation in tolerance in shaping the outcomes of warming tolerance assessments, which arguably are the more widely used vulnerability forecasting tools (both taxonomically and geographically), is less clear. Our review and synthesis asks: is variation in tolerance generally important for warming tolerance-based vulnerability forecasting, and if so, which sources of variation are most important?

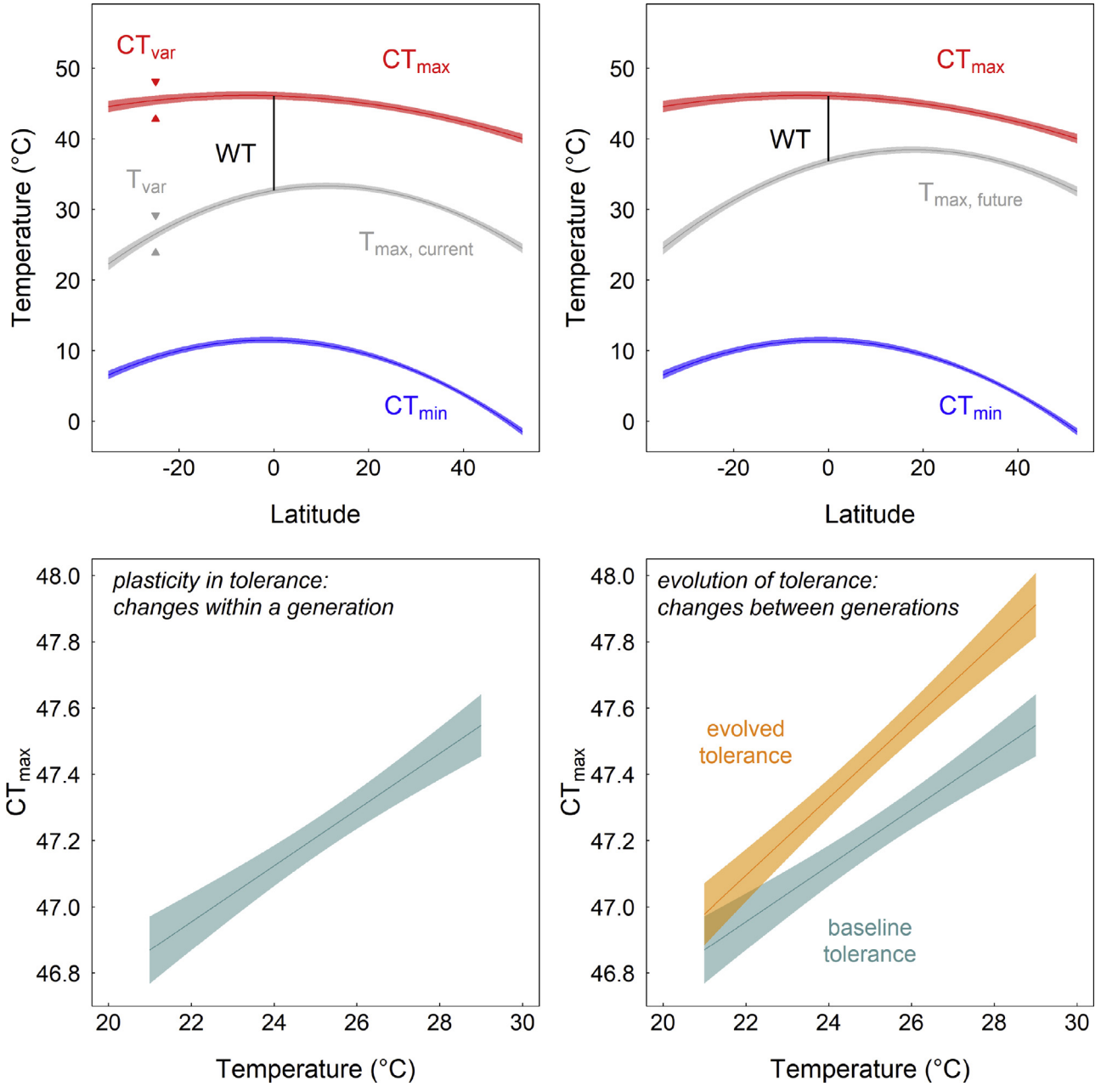
Tolerance variation within generations. Exposure to warmer environmental conditions can lead to the expression of greater heat tolerance within a single generation (Figure 2, Box 1), sometimes manifesting over very short time scales (hours to days) or sometimes over somewhat longer timescales (seasons) [18]. Hypothetically, such phenotypic plasticity could allow organisms to acclimate to global climate change, by allowing organisms to exhibit tolerance values beyond the level of their basal tolerance.

However, this type of plasticity in heat tolerance (i.e. shifts in tolerance under different environmental temperatures) appears to be relatively small (<1°C) for many ectothermic species including insects, suggesting this type of plasticity may have limited capacity to buffer organisms against climate change [19,20••]. Of course, the response of heat tolerance to changes in mean temperature is only one axis along which tolerances may vary. Heat tolerance is also sensitive to the rate at which temperature changes. Dynamic assessments of thermal tolerance, where the temperature is increased by set increments over time, vary by over an order of magnitude with respect to the rate of temperature change, for example, some change the temperature at a rate of less than 0.1°C per minute, and others over 1°C per minute. Faster rates of temperature change often yield higher estimates of heat tolerance, and the difference in estimated heat tolerance using faster and slower rates of temperature change can exceed several °C [21]. For example, a recent comparative study on springtails found that the magnitude of variation in heat tolerance due to differences in the rate at which temperature was increased during the thermal tolerance assay (in some cases, more than 2°C) were greater than the differences due to being reared under different temperature treatments in the laboratory [15••]. Importantly, the effects of variation in the rate of temperature change on thermal tolerance had substantial consequences for patterns of warming tolerance, for example, shifting the greatest vulnerability from low latitude to mid latitude when using slower versus faster rates of temperature change. But is there anything more to this difference beyond experimental artifacts of different rates of temperature change?

In this context, it is worth considering the ecological relevance of variation in the rate of temperature change, specifically whether faster or slower rates of temperature change during the tolerance assay reflect the temperature changes experienced in nature. In general, organisms are confronted with variation in the rate at which environmental temperatures change over time and space; for example, temperature may change at different rates over diurnal and seasonal timescales, or as organisms move throughout thermally heterogeneous environments for critical activities such as foraging [22]. Slower rates of change have been promoted as more ecologically relevant, though with greater potential for experimental artifacts (acclimation during the tolerance assay) compared with faster rates of change. However, there is a growing appreciation for the ecological relevance of faster rates of change [12,23•], and so the question of plasticity in tolerance due to different rates of temperature change is quite relevant to the discussion of vulnerability forecasting.

Tolerance variation between generations. Shifts in tolerance may also manifest across generations (Figure 2, Box 1), though the degree to which heat tolerance can evolve is

Figure 2



Global latitudinal patterns of ant heat tolerance, CT_{max}, cold tolerance, CT_{min} (data from [24]), and maximum temperature during the warmest quarter of the year from WorldClim (left top) and from CMIP5 HADGEM2-ES RCP 8.5 (top right); mean and standard error from mixed effects (to account for phylogenetic non-independence) quadratic models are shown. To maximize coverage of the data, cross-species tolerance patterns are shown, but are generally reflective of intraspecific variation in tolerance across latitude. Warming tolerance (WT) is expressed as the difference between CT_{max} and maximum temperature under current and future climates. Triangles highlight variation in tolerance (CT_{var}), representing variation within and among species, and environmental temperature (T_{var}). The bottom panels use a single species, the acorn ant, *Temnothorax curvispinosus*, to demonstrate variation in CT_{max} within a generation due to plasticity in tolerance across different environmental temperatures (left), and between generations due to selection and evolution of tolerance in response to warmer environmental temperatures (data from [59]).

still an open question. For many ectothermic species generally, and insects in particular [24,25] (but see [8]), there is a strong resemblance among closely related species with respect to their heat tolerance. Although this resemblance (inferred via high phylogenetic signal) is not necessarily indicative of genetic or developmental constraint on the evolution of heat tolerance, it is certainly suggestive [26].

However, related analyses which examine the evolutionary potential (for example, heritability) of heat tolerance of individual species paint a more complex picture. Some studies find evidence of marginal to zero evolutionary potential of heat tolerance [27], though a number of other studies find evidence of significant evolutionary potential of heat tolerance [28,29]. One potential driver of these discrepancies is that evolutionary potential of heat tolerance is sensitive to variation in environmental temperature and rates of temperature change [30,31], reinforcing the importance of assaying thermal environments in nature. Mean heritability of heat tolerance across a range of insect species shows mean heritability to be 0.28 [32], which may appear low, but this value is well within the range for similar traits [33]. Despite some studies finding evidence of heritable variation in heat tolerance, laboratory selection studies on heat tolerance show that genetic variation is exhausted after a limited number of generations [31]. Though here again, these findings must be tempered by growing evidence of rapid evolutionary change in thermal tolerance and thermal performance traits in natural insect populations over contemporary timescales [34•,35,36,37]. In sum, although there is certainly a fair amount of evidence to suggest limited potential for heat tolerance to evolve, there are at least as many counterexamples.

Tolerance variation across space. Tolerances can vary not only over short (ecological) to long (evolutionary) timescales within individual sites, but also across space. Decreasing latitude is generally associated with increasing mean environmental temperature and reduced temperature variability, and as a consequence, mean heat tolerance may be expected to increase while plasticity in heat tolerance may be expected to decrease. However, these expectations are only weakly satisfied in nature — there is a relatively small amount of biogeographic variation in mean heat tolerance ([13,24,25,38,39,40,41], Figure 2; see also for elevational clines [8,42]) and heat tolerance plasticity [19,20••] across a broad range of insects — and in some cases, empirical patterns run counter to these expectations (e.g. greater plasticity at lower latitudes [43]). Based on these patterns, researchers have concluded that this level of variation is insufficient to alter vulnerability forecasts by buffering organisms against climate change [44].

By contrast, latitudinal clines in the evolutionary potential (heritability) of heat tolerance show significant decreases at lower latitudes — the heritability of heat tolerance in temperate regions is nearly double that in tropical regions [32] — reinforcing and potentially exacerbating the greater vulnerability of lower latitude species. Together, these biogeographic patterns suggest important, but contrasting roles for variation in tolerance: the plastic change induced by using faster rates of temperature increase to assess tolerance leads to diminished apparent vulnerability at low latitudes, whereas results from tolerance heritability analysis suggest increased vulnerability at low latitudes.

Interaction of mechanisms underlying tolerance variation. Identifying plastic and evolutionary sources of variation in tolerances is certainly an important goal, but it is also important to recognize that these mechanisms can interact with one another [9•,45,46]. These interactions can be expressed in several ways: for example, increases in mean thermal tolerance can come at the cost of reduced tolerance plasticity [47,48], though support for the generality of this pattern is highly mixed [44]. Behavior may likewise mediate contrasting effects of these mechanisms: behavioral plasticity in response to thermal stress can hide variation from selection and limit potential evolutionary responses [49,50•]. However, the interaction of these mechanisms can also take on a facilitatory role: as global climate change exposes organisms to novel environmental conditions, previously unexpressed genetic variation can be released, and selection may then act on this variation through the process of genetic accommodation (Box 1), though tests of this idea remain very limited [45]. It is difficult to say at this point whether the interaction of plastic and evolutionary mechanisms is of great importance for vulnerability assessments, as research in this area has only recently begun to gather momentum, and has done so outside of considerations of warming tolerance and thermal safety margins.

Synthesis. Two key questions emerge from the consideration of tolerance variation and vulnerability forecasting: Firstly, is the variation in tolerance sufficiently large to modify patterns of warming tolerance? and secondly, is the variation in tolerance sufficiently large (and in the right direction) to keep pace with climate change? For the first question, the answer appears to be yes for some sources of variation — plasticity in tolerance driven by the rate of temperature increase and evolutionary potential (heritability) of tolerance traits can modify patterns of warming tolerance, though in very different ways. Further, it is possible that other sources of variation, such as plasticity across different temperature regimes are undervalued due to issues surrounding experimental design: an obvious example is the assessment of plastic responses often occurs under current temperatures rather than future (stressful) temperatures [51], which may downwardly bias estimation of the plastic response. Any conclusion to the second question thus seems premature at present, as current estimates of tolerance and environmental variation in temperature are clearly in need of further refinement to incorporate plastic and evolutionary mechanisms.

The future of vulnerability forecasting with tolerance traits

Sustained development of large-scale thermal tolerance trait databases such as GlobTherm [52], represent a clear path forward in vulnerability forecasting; however, such trait databases, while beginning to include acclimation (plastic) responses across different temperatures, do not always contain information on other sources of variation in

tolerance. Thus integration of multiple sources of tolerance variation represents a key future direction. Relatedly, research in this area (and therefore the databases) tends to be heavily biased towards heat tolerance [53]. While warming tolerances and thermal safety margins focus on heat tolerance, cold tolerance could be quite important for the response to global change (Figures 1 and 2). For example, relaxation of resource allocation demands on cold tolerance under climate change could potentially influence the expression of heat tolerance. Genetic correlations among tolerance traits could also lead to diminished cold tolerance following selection for improved heat tolerance, leaving organisms vulnerable to extreme (cold) events anticipated under climate change [54•,55]. Further, cold tolerance exhibits much lower phylogenetic signal than heat tolerance, stronger plastic responses to temperature, and is often more strongly related to environmental temperature across latitude [13,20••]. How cold tolerance responds to global change therefore may be quite different from heat tolerance, making overall tolerance responses complex.

A second area for further development is the application of microclimatic assessments of warming tolerance, that is, accounting for the temperatures organisms actually experience (and ideally, how organisms use their thermal habitats) rather than weather station air temperature [13,22,23•,56]. Although we have focused our review on variation in tolerance, the environmental component of warming tolerance is likewise critical, particularly as environmental variation shapes tolerance variation. Because the inclusion of microclimate in the calculation of warming tolerance can either increase [13] or decrease [23•] vulnerability, microclimatic assessments are of much greater value than simple bias corrections. As the integration of different responses to climate change becomes easier with more data and modeling tools, accounting for microclimatic variation due to other compensatory mechanisms that shift the thermal environment such as range shifts and phenological shifts [57,58] may help to further refine vulnerability assessments.

Our aim here was to use insect systems to highlight the potential importance of variation in heat thermal tolerance and its consequences for warming tolerance-based assessments of vulnerability to global change. Although the data available to address this question are in some respects still quite nascent, the research we reviewed here suggests tolerance variation cannot be ignored.

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Conflict of interest statement

Nothing declared

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as

- • of special interest
- •• of outstanding interest

1. Schowalter TD: **Academic Press**. *Insect Ecology: An Ecosystem Approach*. 2016.
2. Koh I, Lonsdorf EV, Williams NM, Brittain C, Isaacs R, Gibbs J, Ricketts TH: **Modeling the status, trends, and impacts of wild bee abundance in the United States**. *PNAS* 2016, **113**:140-145.
3. Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T *et al.*: **More than 75 percent decline over 27 years in total flying insect biomass in protected areas**. *PLOS ONE* 2017, **12**:e0185809.
4. Urban MC: **Accelerating extinction risk from climate change**. *Science* 2015, **348**:571-573.
5. Cooke SJ, Sack L, Franklin CE, Farrell AP, Beardall J, Wikelski M, Chown SL: **What is conservation physiology? Perspectives on an increasingly integrated and essential science**. *Conserv Physiol* 2013, **1** cot001.
6. Madliger CL, Love OP: **The power of physiology in changing landscapes: considerations for the continued integration of conservation and physiology**. *Integr Comp Biol* 2015, **55**:545-553.
7. Urban MC, Bocedi G, Hendry AP, Mihoub J-B, Pe'er G, Singer A, Bridle JR, Crozier LG, Meester LD, Godsoe W *et al.*: **Improving the forecast for biodiversity under climate change**. *Science* 2016, **353**:aad8466.
8. García-Robledo C, Kuprewicz EK, Staines CL, Erwin TL, Kress WJ: **Limited tolerance by insects to high temperatures across tropical elevational gradients and the implications of global warming for extinction**. *PNAS* 2016, **113**:680-685.
9. • Sgrò CM, Terblanche JS, Hoffmann AA: **What can plasticity contribute to insect responses to climate change?** *Annu Rev Entomol* 2016, **61**:433-451.

This review synthesizes the role of plasticity in mediating responses to global climate change, with a specific focus on insect systems.

10. Angilletta MJ: *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford: OUP; 2009.
11. Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR: **Impacts of climate warming on terrestrial ectotherms across latitude**. *PNAS* 2008, **105**:6668-6672.
12. Bonebrake Timothy C, Deutsch Curtis A: **Climate heterogeneity modulates impact of warming on tropical insects**. *Ecology* 2012, **93**:449-455.
13. Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, Huey RB: **Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation**. *PNAS* 2014, **111**:5610-5615.
14. Diamond SE, Sorger DM, Hulcr J, Pelini SL, Toro ID, Hirsch C, Oberg E, Dunn RR: **Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants**. *Glob Change Biol* 2012, **18**:448-456.
15. •• Allen JL, Chown SL, Janion-Scheepers C, Clusella-Trullas S: **Interactions between rates of temperature change and acclimation affect latitudinal patterns of warming tolerance**. *Conserv Physiol* 2016, **4** cow053.

An explicit assessment of how warming tolerance is impacted by variation in tolerance, particularly variation due to differences in rearing temperature, the rate at which temperature was increased during the assessment of heat tolerance and their interaction. For some sources of variation in tolerance, biogeographic patterns of climate vulnerability shift substantially.

16. Hoffmann AA, Chown SL, Clusella-Trullas S: **Upper thermal limits in terrestrial ectotherms: how constrained are they?** *Funct Ecol* 2013, **27**:934-949.

17. Bush A, Mokany K, Catullo R, Hoffmann A, Kellermann V, Sgrò C, McEvey S, Ferrier S: **Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change**. *Ecol Lett* 2016, **19**:1468-1478.

18. Schulte PM, Healy TM, Fangue NA: **Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure**. *Integr Comp Biol* 2011, **51**:691-702.

19. Gunderson AR, Stillman JH: **Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming**. *Proc Biol Sci* 2015, **282**:20150401.

20. •• Sørensen JG, Kristensen TN, Overgaard J: **Evolutionary and ecological patterns of thermal acclimation capacity in Drosophila: is it important for keeping up with climate change?** *Curr Opin Insect Sci* 2016, **17**:98-104.
A synthesis of the work in*Drosophila* systems aimed at understanding the role of thermal acclimation in the response to climate change from local to global scales.

21. Terblanche JS, Hoffmann AA, Mitchell KA, Rako L, le Roux PC, Chown SL: **Ecologically relevant measures of tolerance to potentially lethal temperatures**. *J Exp Biol* 2011, **214**:3713-3725.

22. Woods HA, Dillon ME, Pincebourde S: **The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change**. *J Thermal Biol* 2015, **54**:86-97.

23. • Pincebourde S, Suppo C: **The vulnerability of tropical ectotherms to warming is modulated by the microclimatic heterogeneity**. *Integr Comp Biol* 2016, **56**:85-97.
This study explores how climatic variability over space and time influences the general pattern of increased vulnerability of tropical ectotherms to climate change.

24. Diamond SE, Chick L: **The Janus of macrophysiology: stronger effects of evolutionary history, but weaker effects of climate on upper thermal limits are reversed for lower thermal limits in ants**. *Curr Zool* 2018, **64**:223-230.

25. Kellermann V, Overgaard J, Hoffmann AA, Fløjgaard C, Svenning J-C, Loeschcke V: **Upper thermal limits of Drosophila are linked to species distributions and strongly constrained phylogenetically**. *PNAS* 2012, **109**:16228-16233.

26. Losos JB: **Seeing the forest for the trees: the limitations of phylogenies in comparative biology. (American Society of Naturalists Address)**. *Am Nat* 2011, **177**:709-727.

27. Mitchell KA, Hoffmann AA: **Thermal ramping rate influences evolutionary potential and species differences for upper thermal limits in Drosophila**. *Funct Ecol* 2010, **24**:694-700.

28. van Heerwaarden B, Sgrò CM: **Multivariate analysis of adaptive capacity for upper thermal limits in Drosophila simulans**. *J Evol Biol* 2013, **26**:800-809.

29. Sgrò CM, Overgaard J, Kristensen TN, Mitchell KA, Cockerell FE, Hoffmann AA: **A comprehensive assessment of geographic variation in heat tolerance and hardening capacity in populations of Drosophila melanogaster from eastern Australia**. *J Evolut Biol* 2010, **23**:2484-2493.

30. van Heerwaarden B, Malmberg M, Sgrò CM: **Increases in the evolutionary potential of upper thermal limits under warmer temperatures in two rainforest Drosophila species**. *Evolution* 2016, **70**:456-464.

31. Hangartner S, Hoffmann AA: **Evolutionary potential of multiple measures of upper thermal tolerance in Drosophila melanogaster**. *Funct Ecol* 2016, **30**:442-452.

32. Diamond SE: **Evolutionary potential of upper thermal tolerance: biogeographic patterns and expectations under climate change**. *Ann N Y Acad Sci* 2017, **1389**:5-19.

33. Hoffmann AA, Merilä J, Kristensen TN: **Heritability and evolvability of fitness and nonfitness traits: lessons from livestock**. *Evolution* 2016, **70**:1770-1779.

34. • Brans KI, Jansen M, Vanoverbeke J, Tüzün N, Stoks R, De Meester L: **The heat is on: Genetic adaptation to urbanization mediated by thermal tolerance and body size**. *Glob Change Biol* 2017, **23**:5218-5227.
This study explores rapid evolutionary change in heat tolerance in response to urbanization-driven changes in environmental temperature using*Daphnia* as a model system, and shows how evolution can generate variation in thermal tolerance over contemporary timescales.

35. Geerts AN, Vanoverbeke J, Vanschoenwinkel B, Van Doorslaer W, Feuchtmayr H, Atkinson D, Moss B, Davidson TA, Sayer CD, De Meester L: **Rapid evolution of thermal tolerance in the water flea Daphnia**. *Nat Clim Change* 2015, **5**:665-668.

36. Diamond SE, Chick L, Perez A, Strickler SA, Martin RA: **Rapid evolution of ant thermal tolerance across an urban–rural temperature cline**. *Biol J Linnean Soc* 2017, **121**:248-257.

37. Tüzün N, Op de Beeck L, Brans KI, Janssens L, Stoks R: **Microgeographic differentiation in thermal performance curves between rural and urban populations of an aquatic insect**. *Evol Appl* 2017, **10**:1067-1075.

38. Verble-Pearson RM, Gifford ME, Yanoviak SP: **Variation in thermal tolerance of North American ants**. *J Thermal Biol* 2015, **48**:65-68.

39. Chown SL, Duffy GA, Sørensen JG: **Upper thermal tolerance in aquatic insects**. *Curr Opin Insect Sci* 2015, **11**:78-83.

40. Baudier KM, Mudd AE, Erickson SC, O'Donnell S: **Microhabitat and body size effects on heat tolerance: implications for responses to climate change (army ants: Formicidae, Ecitoninae)**. *J Anim Ecol* 2015, **84**:1322-1330.

41. Kaspari M, Clay NA, Lucas J, Yanoviak SP, Kay A: **Thermal adaptation generates a diversity of thermal limits in a rainforest ant community**. *Glob Change Biol* 2015, **21**:1092-1102.

42. Shah AA, Gill BA, Encalada AC, Flecker AS, Funk WC, Guayasamin JM, Kondratieff BC, Poff NL, Thomas SA, Zamudio KR *et al.*: **Climate variability predicts thermal limits of aquatic insects across elevation and latitude**. *Funct Ecol* 2017, **31**:2118-2127.

43. Seebacher F, White CR, Franklin CE: **Physiological plasticity increases resilience of ectothermic animals to climate change**. *Nat Clim Change* 2015, **5**:61-66.

44. van Heerwaarden B, Kellermann V, Sgrò CM: **Limited scope for plasticity to increase upper thermal limits**. *Funct Ecol* 2016, **30**:1947-1956.

45. Diamond SE, Martin RA: **The interplay between plasticity and evolution in response to human-induced environmental change**. *F1000 Res* 2016, **5**:2835.

46. Kingsolver JG, Buckley LB: **Evolution of plasticity and adaptive responses to climate change along climate gradients**. *Proc R Soc B* 2017, **284**:20170386.

47. Stillman JH: **Acclimation capacity underlies susceptibility to climate change**. *Science* 2003, **301**:65.

48. Gerken AR, Eller OC, Hahn DA, Morgan TJ: **Constraints, independence, and evolution of thermal plasticity: Probing genetic architecture of long- and short-term thermal acclimation**. *PNAS* 2015, **112**:4399-4404.

49. Buckley LB, Ehrenberger JC, Angilletta MJ: **Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change**. *Funct Ecol* 2015, **29**:1038-1047.

50. • Muñoz MM, Losos JB: **Thermoregulatory behavior simultaneously promotes and forestalls evolution in a tropical lizard**. *Am Nat* 2017, **191**:E15-E26.
An examination of the interaction of plastic and evolutionary mechanisms, specifically showing how plasticity in thermoregulatory behavior can both facilitate and retard evolutionary change.

51. Kingsolver JG, Diamond SE, Buckley LB: **Heat stress and the fitness consequences of climate change for terrestrial ectotherms**. *Funct Ecol* 2013, **27**:1415-1423.

52. Bennett JM, Calosi P, Clusella-Trullas S, Martínez B, Sunday J, Algar AC, Araújo MB, Hawkins BA, Keith S, Kühn I *et al.*:

GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. *Sci Data* 2018, **5**:180022.

53. Sunday JM, Bates AE, Dulvy NK: **Thermal tolerance and the global redistribution of animals**. *Nat Clim Change* 2012, **2**:686-690.

54. • Kingsolver JG, Buckley LB: **Quantifying thermal extremes and biological variation to predict evolutionary responses to changing climate**. *Phil Trans R Soc B* 2017, **372**:20160147.
This study demonstrates the importance of climatic variability and extreme temperatures to understand the evolutionary response of a*Colias* butterfly species to climate change, and also considers the role of plasticity in shaping evolutionary responses to climate change.

55. Johannes O, Kearney Michael R, Hoffmann Ary A: **Sensitivity to thermal extremes in Australian Drosophila implies similar impacts of climate change on the distribution of widespread and tropical species**. *Global Change Biol* 2014, **20**:1738-1750.

56. Duffy GA, Coetzee BW, Janion-Scheepers C, Chown SL: **Microclimate-based macrophysiology: implications for insects in a warming world**. *Curr Opin Insect Sci* 2015, **11**:84-89.

57. Estrada A, Morales-Castilla I, Caplat P, Early R: **Usefulness of species traits in predicting range shifts**. *Trends Ecol Evol* 2016, **31**:190-203.

58. Cohen JM, Lajeunesse MJ, Rohr JR: **A global synthesis of animal phenological responses to climate change**. *Nat Clim Change* 2018, **8**:224-228.

59. Diamond SE, Chick LD, Perez A, Strickler SA, Martin RA: **Evolution of thermal tolerance and its fitness consequences: parallel and non-parallel responses to urban heat islands across three cities**. *Proc R Soc B: Biol Sci* 2018, **285**:20180036.